Chapter 34

ROLES OF LITTER-DECOMPOSING AND ECTOMYCORRHIZAL FUNGI IN NITROGEN CYCLING IN THE SCANDINAVIAN CONIFEROUS FOREST ECOSYSTEM

Gösta Lindeberg

Swedish University of Agricultural Sciences
Uppsala, Sweden

I. INTRODUCTION

Among natural terrestrial ecosystems, the forests have the highest sustained productivity because of the effective recycling of nutrient elements (Witkamp and Ausmus, 1976). In this chapter the role of fungi in the recycling of nitrogen will be discussed, particularly with reference to Scandinavian coniferous forests.

One of the most obvious and interesting mycological problems in this ecosystem is the relation between the litter-decomposing fungi and the mycorrhizal fungi associated with the trees. Since this relationship is intimately involved in the transfer of nitrogen from litter to trees, a discussion of this special aspect will be included.

II. AMOUNTS AND COMPOSITION OF LITTER

The litter fall in the Scandinavian coniferous forests is of the order of 2000-4000 kg ha^{-1} $year^{-1}$ (Bonnevie-Svendsen and Gjems, 1957). The humus layer is, in most cases, of the mor type, and the soil profile is a podzol.

The chemical composition of newly fallen pine needle litter is shown in Table 1. Characteristic of this type of litter is that the cell walls of the plant residues

Table 1 Composition (%) of dead needles of *Pinus sylvestris*

Cellulose	30
Hemicelluloses	19
Lignin	28
Water-soluble fraction	14.5
Acetone-soluble fraction	8.4
Total C content	51
Total N content	0.4

Source: Unpublished data of B. Berg (Swedish Coniferous Forest Project).

are strongly lignified, there are large amounts of resins and terpenes, and the C/N ratio is high (>100). The pH of the litter, as well as the F and H layers, is about 4.

III. NITROGEN DISTRIBUTION AND TURNOVER

The nitrogen distribution and turnover in a Scots pine (*Pinus sylvestris*) forest on a sand plain in central Sweden has been extensively studied within the Swedish Coniferous Forest Project, an interdisciplinary ecological research project. Some results are presented in Table 2 (Bringmark, 1978).

The nitrogen content of the vegetation was found to be about twice that in the litter layer. By far the largest part of the nitrogen in the ecosystem is stored in the slowly decomposing humus which occurs not only in the F and H layers but also in considerable amounts in the mineral soil to a depth of at least 30 cm. The nitrogen taken up annually by the vegetation is about one-third of the amount found in the litter. This indicates a slow mineralization rate. In fact, it takes about 7 years for the needles to be completely decomposed. It has been shown (Bringmark, 1978) that about half of the nitrogen taken up by the vegetation goes into the trees and half into the ground cover. The nitrogen input into the system mainly consists of inorganic nitrogen compounds, deposited from the atmosphere. Microbial nitrogen fixation is very small. The total accumulation is about 4 kg of nitrogen per hectare per year. The system is limited by nitrogen (and incidentally also by phosphate). Any nitrogen mineralized is immediately immobilized by microbes, and none remains in solution, so that the drainage loss is practically zero. Thus the metabolism of the fungi and bacteria in the soil layer maintains the nitrogen content of the system.

Table 2 Nitrogen distribution and turnover in a mature Scots pine forest in central Sweden[a]

N content of vegetation (including roots)	184
N content of surface litter	69
N content of root litter	13
N content of humus (F + H) layer	162
N content of mineral soil 0-30 cm	780
N uptake by vegetation	33
N input	
Deposition from the atmosphere	3.6
Microbial fixation	0.4
Drainage loss at 20 cm depth	(0.13)
Accumulated	3.9

[a] Kilograms per hectare per year.

Source: Data from the Swedish Coniferous Forest Project; see Bringmark (1978).

Table 3 Amount of nitrogen in inorganic form and in biomass in humus incubated at 60% WHC[a] and 15°C[b]

	Weeks after start	
	0	28
Amount of nitrogen in:		
Fungi	290	550
Bacteria	156	144
Nematodes	0.03	5.0
Microarthropods	0.02	0.2
Biomass total	446	699
Inorganic N	8.4	13.0
Total movable N	454	712
Total N: 9.8 mg/g DW		
pH 4.0		

[a] WHC = water-holding capacity.

[b] Numbers represent µg N/g DW.

Source: Sohlenius et al. (1976).

An estimate of the amount of nitrogen in inorganic form and in the biomass of the various soil organisms was made in an experiment where samples of humus from the FH layer were incubated in plastic bags for 28 weeks at 15°C and 60% WHC (Sohlenius et al., 1976). Some results are presented in Table 3.

This experiment again shows that the largest part of the nitrogen was bound in the humus components. The "total movable N" (= N bound in organisms + inorganic N) constituted only a small part of the total nitrogen of the humus: 4.6% at the start and 7.3% at the end of the experiment. Some increase in mineralized nitrogen occurred during the experiment: inorganic nitrogen (ammonium nitrogen) rose from 8.4 to 13.0 µg/g dry weight (DW).

Of the nitrogen bound in living organisms, the largest part was found in the fungal mycelia, and the increase in biomass during the experiment was mainly due to fungal growth. The bacterial biomass remained practically unchanged. The amount of nitrogen bound in nematodes and microarthropods was very small.

Because of the apparent importance of the fungi, a critical question is to what extent the fungal mycelia, measured by the Jones and Mollison (1948) technique, are indeed living, i.e., contain living protoplasm, or to what extent they consist of empty cell walls. Söderström (1977), using a method for vital staining of fungal mycelia with fluorescein diacetate, found that during periods of high fungal activity, only 1-5% of the total mycelial mass was metabolically active. Consequently, the relative importance of the bacterial population might be greater than has been thought in forest soil of the mor type.

IV. LITTER-DECOMPOSING FUNGI

Fungi and bacteria compete in and on litter for all that is available to them. The success of each species in a particular environment is dependent on enzyme production, uptake efficiency, growth potential, spreading efficiency, and potential to inhibit the growth of competitors (Goksøyr, 1975).

A. Microfungi

As the different constituents of the litter are gradually decomposed and utilized by microorganisms, a succession of fruiting organs of microfungi, i.e., phycomycetes and ascomycetes, as well as conidial stages of fungi imperfecti, generally occurs. This succession may partly be explained in terms of the time taken for the various species to reach the fruiting or conidial stage, as shown by Harper and Webster (1964) with the fungi developing on rabbit dung. Another cause of this succession is the gradual change in the substrate due to the activities of the decomposers.

Detailed studies on the succession of microfungi on decomposing leaf litter of *Pinus sylvestris* have been carried out by various workers, including Kendrick (1958; summarized by Kendrick and Burges, 1962) and Hayes (1965). Söderström (1975) studied the microfungi occurring on litter and in the different soil horizons in a plantation of Norway spruce (*Picea abies*) in southern Sweden. Reviews of the work on the fungal flora which colonizes coniferous litter were published by Hudson (1968) and Millar (1974). Several authors, however, have emphasized that frequency of isolation is a poor guide to the importance of a fungus species in decomposition (Burges, 1960; Hering, 1967). Therefore, to elucidate the possible role of soil microfungi in decomposition of the various chemical components of plant litter, a number of studies on the enzyme production and decomposing capacity of the soil fungal flora have been carried out (e.g., Domsch and Gams, 1969; Flanagan and Scarborough, 1974; Bååth and Söderström, 1974). In most of these studies, the capacity of the fungi to decompose cellulose, xylan (hemicellulose), pectin, chitin, and protein was tested. A large number of fungi have been found to produce enzymes necessary for the decomposition of these substances.

It has not been possible to test directly the capability of the fungi to decompose lignin in a corresponding way. Flanagan and Scarborough (1974) used an indirect combined test (decolorization of humic acid, darkening of gallic acid, and cellulose decomposition) as an indication of lignin-decomposing ability. So far, however, there is no clear evidence that effective lignin breakdown is brought about by individual microfungi. The present view is that in soil a complex flora of microfungi and bacteria brings about a partial degradation and conversion of lignin into humus.

B. Basidiomycetes

The fungi occurring in the litter and humus layers comprise basidiomycetes as well as the microfungi already discussed. The basidiomycetes themselves comprise litter decomposers and mycorrhizal fungi.

It is not easy to estimate the abundance of basidiomycetes. When the dilution plate technique is used, basidiomycetes are not recorded. When fungal biomass is estimated, the length and average diameter of the hyphae per gram dry weight is determined, but the methods used do not differentiate between different groups of fungi. Although clamped (basidiomycete) and unclamped hyphae may be separated (Miller and Laursen, 1974), several basidiomycetes, e.g., the genus *Suillus* (*Boletus*), lack clamp connections, which makes the discrimination between basidiomycetes and nonbasidiomycetes uncertain. Differentiation between mycelia of litter decomposers and mycorrhizal fungi by morphological methods is not possible. The difficulties are illustrated by a quotation from Flanagan and Scarborough (1974, p. 159), who, referring to the physiological groups of decomposer fungi in tundra, write that "the role of the basidiomycete fungi in the tundra has not been studied, but hyphae with clamp connections show that basidiomycetes account for at least one third of the total soil fungal biomass in the autumn." The fact that research on microfungi and on basidiomycetes mostly seems to proceed with little contact between the different mycologists working in each area exacerbates the difficulties inherent in these studies.

It is well known that certain basidiomycetes, the white rot fungi, can decompose both lignin and cellulose in wood. Falck (1923) suggested that various basidiomycetes growing in forest litter decompose the litter in the same way as the wood-rotting fungi decompose wood, later proving in experiments with pure cultures of a few species that this was the case (Falck, 1930). Lindeberg (1944, 1946) cultured 46 different species of basidiomycetes that occur in nature on decomposing litter (belonging to the genera *Clavaria*, *Clitocybe*, *Collybia*, *Flammula*, *Hypholoma*, *Lepiota*, *Marasmius*, *Mycena*, *Panus*, *Pholiota*, and *Tricholoma*) on sterilized leaf litter and determined the amounts of dry matter, cellulose, and lignin decomposed. All the species studied decomposed the lignin and, with one single exception, the cellulose of the substrate and caused a total dry weight loss of 13-54% in some 6-7 months. Maximum lignin and cellulose losses amounted to 75% and 85%, respectively. Hering (1967) obtained similar results with some other basidiomycetes.

V. IMPORTANCE OF THE C/N RATIO

The carbon/nitrogen ratio of the litter is often used as an indicator of potential decomposability but is, in fact, not a particularly simple concept (Park, 1976). Usually this ratio is expressed as total C/total N and is determined by chemical methods. The ratio thus obtained may be termed the provision ratio (Park, 1976). However, with respect to each species of microorganism that takes part in the decomposition process, only the carbon and nitrogen contents of those constituents of the litter are important which are available to the specific organism in the presence of other microorganisms.

This is illustrated in the "saprophytic sugar fungi" (Burges, 1939), mainly phycomycetes, which are able to utilize sugars and other carbon constituents of plant tissues simpler than cellulose or lignin. The cellulose and lignin of the litter do not represent carbon and energy sources for these organisms. Only after the cellulose has been hydrolyzed by cellulase-producing organisms and soluble decomposition products (glucose, cellobiose) have been produced will further development of the sugar fungi occur. Some of the nitrogen of the litter may be locked up in humus-like compounds at an early stage (Swaby and Ladd, 1962, 1966) and may therefore be unavailable to the sugar fungi.

The lignin- and cellulose-decomposing fungi are probably able to utilize a portion of the nitrogen bound in these compounds, which are to a high degree resistant to attacks by other microorganisms (cf. Sec. VII, below), and hence have a larger nitrogen supply than the sugar fungi. However, the effective C/N ratio of the substrate available to the aforementioned fungi will be much higher than the C/N ratio of the substrate available to the sugar fungi.

VI. NITROGEN NUTRITION OF LITTER-DECOMPOSING BASIDIOMYCETES

Nitrogen nutrition of the litter-decomposing basidiomycetes has been studied by several workers, but many problems are still unsolved.

As a rule, these fungi are able to use ammonium nitrogen as the sole nitrogen source, whereas only a few of the species investigated can utilize nitrate (Lindeberg, 1944; Lundeberg, 1970). The ability of the same fungi to utilize amino acids has not been extensively studied. In several species, however, glutamic and aspartic acids as well as asparagine could be used as nitrogen sources (Norkrans, 1950). Other amino acids were utilized only by certain species.

In *Marasmius perforans*, which decomposes spruce needles, an addition of pyridoxine was required for the utilization of casein hydrolyzate and individual amino acids (Lindeberg and Lindeberg, 1964). However, requirements for specific amino acids seem to be uncommon among these fungi.

Growth of the lignin- and cellulose-decomposing fungi will be limited by the available nitrogen. It has been shown by Cowling (1970) that the wood-destroying fungi economize on their limited nitrogen resources by recycling available nitrogen in a dynamic and continuous system of autolysis of less active cells and reutilization of nitrogenous constituents by more active mycelia without significant loss. To what extent the litter-decomposing basidiomycetes are able to conserve their nitrogen supply in a similar way is not known. A recycling of nitrogen within the mycelia of these fungi seems, however, most probable.

VII. ROLE OF FUNGI IN THE TRANSFER OF NITROGEN TO TREE ROOTS

Since the classical works of Frank (1885) and Melin (1917), the beneficial effect of ectomycorrhizae to trees has been well established. Using the tracer technique, Melin and Nilsson (1952, 1953) showed that ^{15}N, absorbed as ammonium ions or glutamic acid by the mycelium of the fungal symbiont, was translocated to the host plant, whereas ^{14}C-tagged products of photosynthesis were translocated to the fungal symbiont (Melin and Nilsson, 1957).

On the other hand, the hypothesis that the ectomycorrhizae of forest trees might function as nitrogen-fixing organs has not been supported by critical experimental work, although the possibility remains that nitrogen-fixing bacteria may to some extent be stimulated in the rhizosphere of mycorrhizae (Harley, 1969).

Since the findings of Melin (1925) that various mycorrhizal fungi could use essentially only glucose as a carbon and energy source, the restricted ability of these fungi to utilize organic compounds other than a few mono- and disaccharides and, sometimes, starch has been confirmed by several authors (Norkrans, 1950; Palmer and Hacskaylo, 1970). Björkman (1942) demonstrated a correlation between the frequency of mycorrhizae and the concentration of soluble carbohydrates in the roots of *Pinus sylvestris*.

Two factors have been suggested as causing a rapid flow of assimilates from the host tree to the mycorrhizal fungus: (1) Lewis and Harley (1965) found that the mycorrhizal fungus in beech mycorrhiza absorbed sugars from the host and converted them into forms (mannitol, trehalose, and glycogen) that were unavailable for reciprocal flow. This "sink" in the fungal layer effectively contributes to the rapid translocation of photosynthate to the fungal sheath. (2) Auxin secretion of the mycorrhizal fungi may possibly enhance translocation of sugars to the infected roots from the upper parts of the tree (Meyer, 1974).

The mycorrhizal fungi which have so far been studied in the laboratory are mostly unable to produce extracellular enzymes such as cellulase, pectinase, proteinase, and laccase (Lindeberg, 1948; Norkrans, 1950; Lyr, 1963; Lundeberg, 1970; Lindeberg and Lindeberg, 1977). Lyr (1963) concluded that in these fungi, compared with litter and wood decomposers, the biosynthetic power is more specifically directed toward mycelial than toward ectoenzyme production. It seems probable that this is facilitated by the ample supply of sugars that the symbionts obtain from the trees.

According to Goksøyr (1975, p. 232), the ecological importance of the mycorrhizal fungi probably lies on the primary production side, in relation to mineral nutrition: "These fungi should then, in an ecological sense, be considered as extensions of the plant root system, and their biomass and growth (including fructifications) as an energy expenditure by the plant, necessary to obtain a sufficient supply of inorganic nutrients."

An estimation of the production of fruit bodies of mycorrhizal fungi which may occur in a pine forest is given by Romell (1939). During one season, the fruit bodies of *Boletus* (*Suillus*) *bovinus* amounted to 180 kg DW (containing about 5 kg nitrogen) per hectare. The formation of this quantity of fruit bodies would require about 400 kg of carbohydrates, i.e., the equivalent of 1 m^3 of timber. Lower estimates for the production of fruit bodies by mycorrhizal fungi were made by Hering (1966) and Richardson (1970). Harley (1971) suggests that the values given by Romell may be accepted as representing the upper limit of the carbon drain due to mycorrhizal fungi.

Because mycorrhizal fungi do not depend on litter for their carbon and energy, they compete successfully with litter-decomposing fungi for available inorganic nutrients. The effectiveness of the nitrogen uptake of the mycorrhizal fungi probably contributes to the prevention of leakage of nitrogen from the forest ecosystem.

The question as to what extent actively growing mycelia of litter-decomposing and mycorrhizal basidiomycetes occur within the same layers of litter is as yet unresolved. It is generally assumed that the mycelia of mycorrhizal fungi extend from the mycorrhizal roots into the surrounding soil so that a larger volume of soil is penetrated and the absorption of water and nutrient salts is increased. According to Bowen (1968), those mycorrhizal fungi which form mycelial strands are especially able to exploit the soil. On the other hand, there is some evidence that exploitation of the litter layers by mycorrhizal fungi may be inhibited. Cold water extracts of leaf litter contain substances which inhibit the growth of various ectomycorrhizal fungi (Melin, 1946), whereas the growth of litter-decomposing fungi is strongly stimulated by the same extracts (Lindeberg, 1944). The main growth-inhibiting components of leaf litter of aspen (*Populus tremula*) were identified by Olsen et al. (1971) as benzoic acid and catechol. These compounds, when added alone to synthetic nutrient solutions, had a strong inhibiting effect on mycorrhizal fungi, e.g., *Boletus* (*Suillus*) *luteus* and *B. variegatus*, but only a weak inhibiting effect on litter-decomposing fungi, e.g., *Marasmius perforans* and *M. scorodonius* (Table 4). In the presence of aspen leaf litter extract, growth of the litter decomposers was strongly stimulated even after an extra addition of benzoic acid and catechol.

The sensitivity of mycorrhizal fungi to aromatic compounds in litter probably restricts their growth in fresh litter. However, the litter-decomposing basidiomycetes generally produce extracellular phenol oxidases (Lindeberg, 1948) and probably

Table 4 Effect on growth of fungi of catechol (Cat.), benzoic acid (BA), and extract of aspen leaf litter[a]

	Mycorrhizal fungi		Litter decomposers	
Addition	*Boletus luteus*	*Boletus variegatus*	*Marasmius perforans*	*Marasmius scorodonius*
None	100	100	100	100
Cat.	3	16	44	66
Cat. + BA	0.6	2	51	69
Extract	0.9	57	617	520
Extract + Cat.	1	7	200	456
Extract + Cat. + BA	0.9	2	295	457

[a] Concentration: Cat. and BA 0.5 mM, extract 20% v/v. Dry weight in percentage of control.

Source: Olsen et al. (1971).

cause an oxidative breakdown of aromatic compounds in the litter. This may suggest that the aromatic inhibitors are gradually eliminated so that the mycorrhizal fungi can penetrate somewhat further into the litter layers, where they could compete for mineralized nitrogen.

A suppressing effect of mycorrhizal roots of *Pinus radiata* on litter decomposition was reported by Gadgil and Gadgil (1971, 1975). These authors claim that the ectomycorrhizal fungi permeate the litter, inhibit the activity of the litter decomposers, and indirectly contribute to the formation of mor humus. Mycorrhizal control of litter decomposition would act as a conservation mechanism whereby the nutrient pool in the upper soil layers is protected against losses by leaching or volatilization. In view of the differences between mycorrhizal and litter-decomposing fungi with respect to the availability of their respective energy sources (Harley, 1971), it seems possible that the former group might be favored in the competition for nitrogen and other nutrients, which may explain the effects observed by Gadgil and Gadgil (1971). To what extent the conclusions of Gadgil and Gadgil are compatible with the aforementioned inhibiting effects of litter extracts is not quite clear.

Certainly, more research is needed on the relations between mycorrhizal and litter-decomposing basidiomycetes in the litter and humus layers.

In forest management it is important to know to what extent mobilization of the large pool of nitrogen bound in humus may be enhanced and which soil organisms are able to mineralize this type of nitrogen. It has been suggested that mycorrhizal fungi may contribute to the mineralization and that this activity might be one of the advantages of mycorrhizal formation as summarized by Lundeberg (1970).

This problem has been studied experimentally by Lundeberg (1970). Mor humus from a pine stand was labeled with ^{15}N by storage for 6 months at optimum temperature and humidity after the addition of [^{15}N]ammonium sulfate and glucose. To eliminate nonincorporated nitrogen, the humus was extracted with dilute sulfuric acid. The capability of different ectomycorrhizal and litter-decomposing basidiomycetes to utilize the organically bound nitrogen in the humus was tested in culture experiments. The litter-decomposing species but none of the mycorrhizal species were able to utilize this nitrogen.

Lundeberg (1970) also studied the capability of mycorrhizal and litter-decomposing fungi to stimulate the translocation of nitrogen bound in humus to pine seedlings grown in ^{15}N-containing humus. None of the mycorrhizal fungi tested had any significant effect. Only in the presence of one litter-decomposing nonmycorrhizal isolate of *Boletus subtomentosus* did the seedlings show considerably stimulated growth. With other isolates of litter decomposers, no positive results were obtained.

VIII. CONCLUSIONS

The quantitative roles of different groups of fungi in decomposition of various types of litter is not known. The enzymatic and other metabolic potentials of different microfungi have been studied, and enzymes catalyzing the breakdown of cellulose, hemicelluloses, pectin, chitin, and protein have been found. Lignified cellulose in forest litter is probably attacked to a large extent by basidiomycetes capable of lignin and cellulose decomposition. Nitrogen is a limiting factor in litter decomposition, and a large part of the available nitrogen will be utilized and immobilized in mycelia and fruit bodies of the fungi. These mycelia and fruit bodies will serve as sources of food for the soil fauna, resulting in a release of nutrients in feces. Lytic bacteria and actinomycetes will contribute to the decomposition of mycelia, and autolysis is most probably part of a mechanism for recycling of nitrogen within mycelia of higher fungi. The transfer of nitrogen from the decomposers to the roots of trees and ground cover vegetation is very effective and is probably due predominantly to uptake by mycorrhizal fungi. The effective conservation of nitrogen within the forest ecosystem is probably also due, in part, to the activity of bacteria in the humus layer. The humus contains a large pool of bound nitrogen. Preliminary experiments indicate that certain litter-decomposing basidiomycetes but not the mycorrhizal fungi may contribute to the mobilization of this nitrogen. The relationships between the litter-decomposing and the mycorrhizal fungi should be further studied.

REFERENCES

Bååth, E., and Söderström, B. (1974). Decomposition of cellulose, xylan, chitin, and protein by microfungi isolated from coniferous forest soils. *Swedish Coniferous Forest Project, Internal Rep. No. 19* (Uppsala).

Björkman, E. (1942). Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. *Symb. Bot. Upsal.* 6(2): 1-191.

Bonnevie-Svendsen, C., and Gjems, O. (1957). Amount and chemical composition of the litter from larch, beech, Norway spruce and Scots pine stands and its effect on the soil. *Meddl. Norske Skogforsöksvesen No. 48*.

Bowen, G. D. (1968). Phosphate uptake by mycorrhizas and uninfected roots of *Pinus radiata* in relation to root distribution. *Trans. 9th Int. Congr. Soil. Sci. 1968* Vol. 2, p. 219.

Bringmark, L. (1978). A bioelement budget of an old Scots pine forest in central Sweden. *Silva Fennica 11*(3): 201-209.

Burges, A. (1939). Soil fungi and root infection. *Broteria 8*: 64-81.

Burges, A. (1960). Dynamic equilibria in the soil. In *The Ecology of Soil Fungi*, D. Parkinson and J. S. Waid, (Eds.). Liverpool University Press, Liverpool, England, pp. 185-191.

Cowling, E. (1970). Nitrogen in forest trees and its role in wood deterioration. *Acta Univ. Upsal. 164*.

Domsch, K. H., and Gams, W. (1969). Variability and potential of a soil fungus population to decompose pectin, xylan, and carboxymethylcellulose. *Soil Biol. Biochem. 1*: 29-36.

Falck, R. (1923). Erweiterte Denkschrift über die Bedeutung der Fadenpilze für die Nutzbarmachung der Abfallstoffe zur Baumernährung im Walde. *Mykol. Untersuch. Ber. 2*: 38-72.

Falck, R. (1930). Nachweise der Humusbildung und Humuszehrung durch bestimmte Arten höheren Fadenpilze im Waldboden. *Forstarch. 6*: 366-377.

Flanagan, P. W., and Scarborough, A. (1974). Physiological groups of decomposer fungi on tundra plant remains. In *Soil Organisms and Decomposition in Tundra.* IBP Tundra Biome Steering Committee, Stockholm, pp. 159-181.

Frank, B. (1885). Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. *Ber. Deut. Bot. Ges. 3*: 128-145.

Gadgil, R. L., and Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature 233*: 133.

Gadgil, R. L., and Gadgil, P. D. (1975). Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. *N.Z. J. For. Sci. 5*: 31-41.

Goksøyr, J. (1975). Decomposition, microbiology, and ecosystem analysis. In *Fennoscandian Tundra Ecosystems. Ecol. Stud. No. 16*, F. E. Wielgolaski (Ed.). Springer-Verlag, New York, pp. 230-238.

Harley, J. L. (1969). *The Biology of Mycorrhiza*, 2nd ed. Plant Science Monographs, N. Polunin (Ed.). Hill, London.

Harley, J. L. (1971). Fungi in ecosystems. *J. Ecol. 59*: 653-668.

Harper, J. E., and Webster, J. (1964). An experimental analysis of the coprophilous fungus succession. *Trans. Brit. Mycol. Soc. 47*: 511-530.

Hayes, A. J. (1965). Some microfungi from Scots pine litter. *Trans. Brit. Mycol. Soc. 48*: 179-185.

Hering, T. F. (1966). The terricolous higher fungi of four Lake District woodlands. *Trans. Brit. Mycol. Soc. 49*: 369-383.

Hering, T. F. (1967). Fungal decomposition of oak leaf litter. *Trans. Brit. Mycol. Soc. 50*: 267-273.

Hudson, H. J. (1968). The ecology of fungi on plant remains above the soil. *New Phytol. 67*: 837-874.

Jones, P. C. T., and Mollison, P. E. (1948). A technique for the quantitative estimation of soil microorganisms. *J. Gen. Microbiol. 2*: 54-69.

Kendrick, W. B. (1958). Ph.D. thesis, University of Liverpool, England.

Kendrick, W. B., and Burges, A. (1962). Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia 4*: 313-344.

Lewis, D. H., and Harley, J. L. (1965). Carbohydrate physiology of mycorrhizal roots of beech. III. Movement of sugars between host and fungus. *New Phytol. 64*: 256-269.

Lindeberg, G. (1944). Über die Physiologie ligninabbauender Bodenhymenomyzeten. *Symbolae Bot. Upsal. 8*(2): 1-183.

Lindeberg, G. (1946). On the decomposition of lignin and cellulose in litter caused by soil-inhabiting hymenomycetes. *Ark. Bot. 33A*: No. 10.

Lindeberg, G. (1948). On the occurrence of polyphenol oxidases in soil-inhabiting basidiomycetes. *Physiol. Plant. 1*: 196-205.

Lindeberg, G., and Lindeberg, M. (1964). The effect of pyridoxine and amino acids on the growth of *Marasmius perforans* Fr. *Arch. Microbiol. 49*: 86-95.

Lindeberg, G., and Lindeberg, M. (1977). Pectinolytic ability of some mycorrhizal and saprophytic hymenomycetes. *Arch. Microbiol. 115*: 9-12.

Lundeberg, G. (1970). Utilization of various nitrogen sources, in particular bound soil nitrogen, by mycorrhizal fungi. *Stud. For. Suec. 79*: 1-95.

Lyr, H. (1963). Zur Frage des Streuabbaues durch ektotrophe Mykorrhizapilze. In *Mykorrhiza: Internationales Mykorrhizasymposium, Weimar, 1960.* Fischer, Jena, pp. 123-145.

Melin, E. (1917). Studier över de norrländska myrmarkernas vegetation. *Norrl. Handbibl.* (Uppsala) *No. 7.*

Melin, E. (1925). *Untersuchungen über die Bedeutung der Baummykorrhiza.* Fischer, Jena.

Melin, E. (1946). Der Einfluss von Waldstreuextrakten auf das Wachstum von Bodenpilzen, mit besonderer Berücksichtigung der Wurzelpilze von Bäumen. *Symbolae Bot. Upsal. 8*(3): 1-116.

Melin, E., and Nilsson, H. (1952). Transfer of labelled nitrogen from an ammonium source to pine seedlings through mycorrhizal mycelium. *Svensk Bot. Tidskr. 46*: 281-285.

Melin, E., and Nilsson, H. (1953). Transfer of labelled nitrogen from glutamic acid to pine seedlings through the mycelium of *Boletus variegatus* (Sw.) Fr. *Nature 171*: 134.

Melin, E., and Nilsson, H. (1957). Transport of C^{14} labelled photosynthate to the fungal associate of pine mycorrhiza. *Svensk Bot. Tidskr. 51*: 166-186.

Meyer, F. H. (1974). Physiology of mycorrhiza. *Ann. Rev. Plant Physiol. 25*: 567-586.

Millar, C. S. (1974). Decomposition of coniferous leaf litter. In *Biology of Plant Litter Decomposition*, C. H. Dickinson and G. J. F. Pugh (Eds.). Academic Press, New York, pp. 105-128.

Miller, O. K., Jr., and Laursen, G. A. (1974). Belowground fungal biomass on US tundra biome sites at Barrow, Alaska. In *Soil Organisms and Decomposition in Tundra.* IBP Tundra Biome Steering Committee, Stockholm, pp. 151-158.

Norkrans, B. (1950). Studies in growth and cellulolytic enzymes of *Tricholoma. Symbolae Bot. Upsal. 11*(1): 1-126.

Olsen, R., Odham, G., and Lindeberg, G. (1971). Aromatic substances in leaves of *Populus tremula* as inhibitors of mycorrhizal fungi. *Physiol. Plant. 25*: 122-129.

Palmer, J. G., and Hacskaylo, E. (1970). Ectomycorrhizal fungi in pure culture. I. Growth on single carbon sources. *Physiol. Plant. 23*: 1187-1197.

Park, D. (1976). Carbon and nitrogen levels as factors influencing fungal decomposers. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, 17th Symp. Brit. Ecol. Soc. Blackwell Sci. Publns., Oxford, England, pp. 41-59.

Richardson, M. J. (1970). Studies on *Russula emetica* and other agarics in a Scots pine plantation. *Trans. Brit. Mycol. Soc. 55*: 217-229.

Romell, L. G. (1939). Barrskogens marksvampar och deras roll i skogens liv. *Svenska SkogsvFör. Tidskr.* pp. 348-375.

Söderström, B. E. (1975). Vertical distribution of microfungi in a spruce forest soil in the south of Sweden. *Trans. Brit. Mycol. Soc. 65*: 419-425.

Söderström, B. E. (1977). Vital staining of fungi in pure cultures and in soil with fluorescein diacetate. *Soil Biol. Biochem. 9*: 59-63.

Sohlenius, B., Berg, B., Clarholm, M., Lundkvist, H., Popović, B., Rosswall, T., Staaf, H., Söderström, B., and Wirén, A. (1976). Mineralization and soil organism activity in a coniferous humus: A model building experiment. *Swedish Coniferous Forest Project, Internal Rep. No. 40*, 51 pp.

Swaby, R. J., and Ladd, J. N. (1962). Chemical nature, microbial resistance, and origin of soil humus. *Trans. Joint Meeting Comm. IV and V, Int. Soc. Soil Sci.* pp. 197-202.

Swaby, R. J., and Ladd, J. N. (1966). Stability and origin of soil humus. In *The Use of Isotopes in Soil Organic Matter Studies.* Spec. suppl. to *J. Appl. Rad. Isotopes*, pp. 153-159.

Witkamp, M., and Ausmus, B. S. (1976). Processes in decomposition and nutrient transfer in forest systems. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, 17th Symp. Brit. Ecol. Soc. Blackwell Sci. Publns., Oxford, England, pp. 375-396.